

Extreme Primates: Ecology and Evolution of Asian Lorises

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Asia's slow and slender lorises (*Nycticebus* and *Loris*) are among nature's most extreme primates. Until recently, it was not understood why lorises have such huge forward-facing eyes, strange steady climbing locomotion, tiny dependent babies, and a bite that potentially can kill a human! Indeed, early studies described them as slow, solitary, and boring. Twenty years of field research now indicate that lorises are among the most intriguing mammal species.

Few primate species are actually known by their descriptor. One mangabey and one gibbon are known to be "agile," but most must be satisfied with being grey or brown or, if they are lucky, mustached or even bald. However, one group of primates, the lorises, has names that in almost every language describe some aspect of their behavior or appearance. Local people have long had their own names for these primates. In India they were known as the bashful ones or the forest babies, in Borneo as the shy ones, in Sumatra and Thailand as the wind monkeys, and

in Java as the little firefaces or moonfaces. *Loris* itself comes from the old Dutch *Loeris*, meaning clown; it is not clear whether early Dutch explorers thought lorises were funny or if they found their circumocular patches reminiscent of a clown's artistry. When explorers first discovered lorises in 1770, they affiliated them with the Neotropical sloths because of their seemingly slow movements.¹ Thus, in English, the term "slow loris" was born, and has been used for slow and slender lorises alike. At the same time, the very name "slow loris" conjures misperceptions about the nature of how lorises live in the wild. The naturalist W. W. Phillips² noted this misplaced judgment in 1905, when he wrote of *Loris*: "Certainly in the glare of the sun, and bewildered by unusual surroundings and noise, he is hesitating and cautious in the extreme; - he is nervous, defenceless and rather pathetic, knowing not which way to turn to escape. But see him at dusk, in familiar surroundings and he is a very different animal. Wonderfully agile and absolutely noiseless he arrives like a fleeting shadow and departs again in ghost-like silence - a true spectre of the gloom to the lesser folk of the woodlands, on whom he preys (Still, 1905:206)."²

Asia's slow and slender lorises are certainly among the most committed tree dwellers of all primates. Com-

prising two genera, *Loris* and *Nycticebus*, the ten currently recognized species (Box 1) make up the subfamily Lorisinae (Fig. 1), having split from their African sister taxa, the pottos (Perodicticidae) and the galagos (Galagidae) approximately 40 million years ago.³ An inability to leap means that coming to the ground is rarely an option for these specialized climbers. The abundant anatomical consequences of this nonsaltatory locomotion and other distinctly primate-like characteristics (Box 2) have long attracted the interest of anatomists to these genera. In particular, lorises, which have the longest life histories of primates of their body size, have been described as having extremely modified grasping hands and feet and the highest degree of stereoscopic vision. Indeed, even before any field studies were conducted, Cartmill¹⁰ stated that lorises "are more highly specialized than any other living strepsirrhine for the mode of life whose adoption led to the differentiation of the order Primates from the other placentals." Now, nearly two decades of field studies allow the first synthesis of how lorises use these traits to adapt to an arboreal lifestyle and why, rather than describing lorises as being boring or sloth-like, we can describe them as extreme primates.

A LORIS SUPERHIGHWAY

Most authors agree that the fine branch niche is the adaptive stage on which early primates evolved their major traits, key among them being their prehensile hands and feet, which they use to grasp slender

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Box 1. Diversity Among Living Lorises

The currently recognized species of slow and slender lorises, including their range of countries and the minimum and maximum recorded body mass for each species. Morphology, genetics, and behavior all point to more species within this family.

Lorinae	Common Name	Geographic Distribution	Body Mass (wild) (g)
<i>Loris lydekkerianus</i>	Mysore slender loris	South India; Sri Lanka	225–320
<i>L. tardigradus</i>	red slender loris	Sri Lanka	105–170
<i>Nycticebus bengalensis</i>	Bengal slow loris	Burma, Bhutan, Cambodia, China, India, Laos, Thailand, Vietnam	1,140–2,100
<i>N. pygmaeus</i>	pygmy slow loris	Cambodia, China, Laos, Vietnam	360–580
<i>N. coucang</i>	greater slow loris	Sumatra, peninsular Malaysia, Thailand, Singapore	635–850
<i>N. javanicus</i>	Javan slow loris	Indonesia (Java)	750–1,150
<i>N. menagensis</i>	Philippine slow loris	Brunei, Indonesia, Malaysia, Philippines	265–800
<i>N. borneanus</i>	Bornean slow loris	Borneo	360–580
<i>N. kayan</i>	Kayan slow loris	Borneo, Malaysia	500–700
<i>N. bancanus</i>	Sody's slow loris	Banka, Belitung Indonesia	?



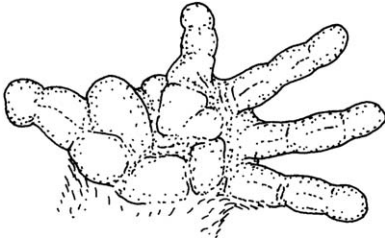
Figure 1. Some of the living Asian lorises. Clockwise from upper left, *Nycticebus javanicus*, showing a striking facial mask (K. A. I. Nekaris); *N. bengalensis* (N. Das), showing cantilever posture; *N. pygmaeus*, with hands firmly gripped around bamboo substrate (K. A. I. Nekaris); *Loris tardigradus tardigradus* in dense understory vegetation (K. A. I. Nekaris); *L. lydekkerianus nordicus*, parked juvenile (K. A. I. Nekaris); *N. menagensis*, showing camouflage against a gum-producing trunk (R. Munds); *N. coucang* rescued from the pet trade (K. A. I. Nekaris). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

twigs, vines, and lianas.^{11,12} The size of these early primates is contested, with the consensus pointing toward a small-bodied primate in the range of a 50-g mouse lemur.¹³ Others offer very different estimates. Based on

recent tiny Eocene fossil finds, Gebo¹⁴ has argued that basal primates might be the size of a 10–15 g shrew, whereas Soligo and Martin¹⁵ suggest that in order for prehensile hands and their associated flat nails

to be useful, we should expect the first primates to be in size classes of 1,000 g or more. Interestingly, the lorises bracket this entire range. With *Loris* giving birth to 9-g infants and *Nycticebus* to 43-g infants that slowly

Box 2. Unique Loris Characteristics, Including a picture of the Hand of *N. coucang* (by H. Schulze)



The lorises have a spectacular array of morphological characteristics that set them apart from other primates. Fewer caudal vertebrae, more numerous thoracic vertebrae, and transpedicular foramina of the thoracic vertebrae help give lorises

a sinuous, snake-like way of moving that is the envy of tai-chi enthusiasts.⁴ Large humeral and femoral articulations,⁵ combined with highly mobile ankles and wrists,⁶ allow them to twist and turn and grab handfuls of branches in their complex arboreal environment, stretching across unlikely gaps that a “normal” primate would leap across. Grasping hands and feet with a pollex and hallux that can be adducted 180° from the other digits allow them to hold on to branches and prey tightly. Their frontated and upwardly rotated orbits are among the most conver-

gent of any primate. All lorises, no matter their size, have a basal metabolic rate 50% of the value predicted by the Kleiber standard.⁷ Lorises are equipped with an array of specialized scent glands that they use to communicate complex olfactory messages to conspecifics.⁸ One of these, the brachial gland, exudes a secretion when the loris is threatened⁹; when combined with saliva, the brachial oil becomes toxic to some animals, making the slow loris the world’s only venomous primate.

develop into the smallest 100 g *Loris* adults and the largest 2100 g *Nycticebus* adults, these two genera cover an extreme range of sizes for the otherwise relatively unspicuous Asian lorises. Indeed, *Nycticebus* appears to be the only primate genus with almost an order of magnitude difference in adult body mass between species (Box 1). Taking into account the mass of juveniles, this difference is even more extreme.

Despite differences in species size, loris hands and feet, be they slender or slow, are remarkably similar, albeit peculiar. In terms of relative lengths of digits, by listing them in order of decreasing length, or the digital formula, lorises ally with the other lemurs at 4:3:5:2:1.¹³ The second digit, replete with toilet claw on the foot, is extraordinarily reduced in comparison; this produces a pincer-like action that allows a loris to hold tightly to branches (Box 2).⁶ This grasp has been deemed primitive and opposable, with the first digit opposing the fifth digit around a substrate and all four lateral digits contributing to force production during grasping.¹⁶ In the foot, this arrangement is associated with an enlarged peroneal process on the first metatarsal that has been implicated as being important for powerful grasping (but see Kingston and colleagues¹⁷). These unusual features are coupled with main limb arteries form-

ing vascular bundles known as *retia mirabilia*, a trait that allows blood to flow even when the animal remains still. Several hypotheses have been put forward as to why lorises have evolved these extreme grasping abilities: They evolved to suit an undergrowth continuous niche where leaping simply was not necessary¹⁸; as a cryptic anti-predator strategy^{19–21}; as a mechanism to cope with a low-quality diet and thus occupy a divergent niche from then sympatric galagos.⁸ More recently, with the revelation that slow lorises (*Nycticebus*) are among the most highly exudativorous of all primates, extreme grasping in combination with u-shaped hind limbs has been attributed to the need to gouge for extended periods on wide trunks.²²

Intriguingly, most captive examinations of this remarkable locomotor pattern have been made of single animals in a small cage^{23,24} or animals moving on a single pole, either urged forward with rewards²⁵ or encouraged to move freely in this unnatural situation^{26,27} (but see Nekaris and Stevens²⁸ for animals offered multiple substrates). Although these studies have built a picture in which lorises can move quickly and even “race-walk” up to 1.65 m/sec,²⁹ and help us to understand loris gait kinematics, they bear little resemblance to what a wild

loris looks like when it moves. Please see videos 1–3 (https://www.youtube.com/watch?v=ghs_8_PqEeo, https://www.youtube.com/watch?v=s_Y96nGQtXA, <https://www.youtube.com/watch?v=Oys5XUTxwms>).

Influenced by descriptions of sloth-like lorises, primarily kept as diurnal pets by colonial plantation owners, the first wild studies of lorises also contributed to the myth of the “slow” loris, which is difficult to shatter. After Petter and Hladik³⁰ conducted the first nine-day study of grey slender lorises (*Loris lydekkerianus nordicus*) in Sri Lanka, they suggested that lorises were solitary, moved only 15–20 m per night, primarily dwelled in a single tree, and were separated from one another by 100 m. They suggested the animals would normally be found at a height of 2–3 m, rarely at 5–10 m. In the first longer study of the greater slow loris (*Nycticebus coucang*) in Malaysia, Barrett³¹ managed to catch a single female loris and monitor it by a radio collar for five days, in that short time increasing the loris’ documented home range to 5–10 ha.

Seven species of slow and slender loris have now been studied to some degree, and some seeming loris universals have emerged. A loris is never more stressed than when it is holding on to one single branch, at which

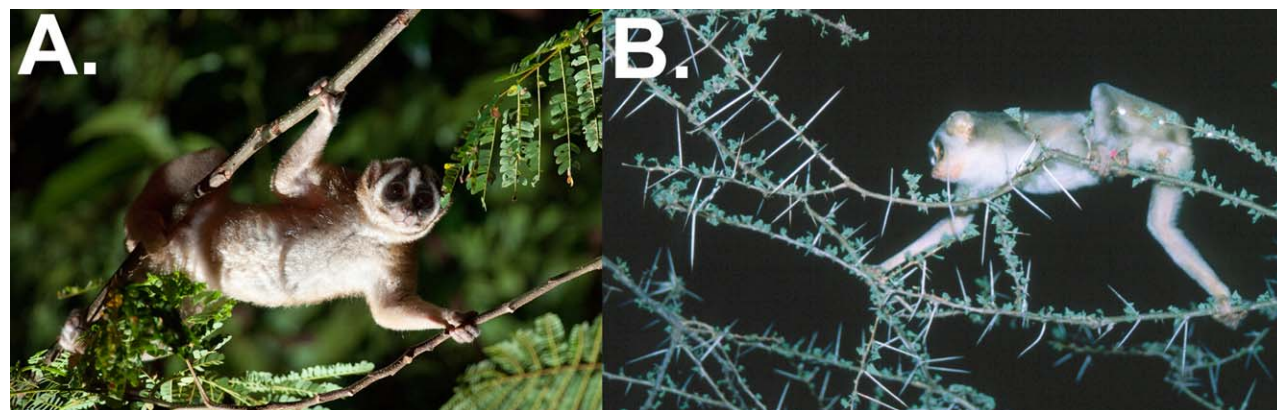


Figure 2. Neither slow (a) nor slender (b) lorises can leap. Instead, they stretch across their habitats by grabbing bundles of small branches, using a variety of hanging and bridging postures. Occasionally a loris clings to a single branch or trunk but, most commonly, they cling to three or more substrates at once. (Left Photo by A. Walmsley; Right photo by K.A.I Nekaris). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

time it moves slowly and cautiously. It may use a long vine or bamboo stem to cross a large gap but, in most cases, the loris uses its long limbs to hold on to multiple branches at once (Fig. 2).^{32,33} The grasping hands may be used to cling during high winds or if a predator tries to shake a loris from a tree.³⁴ Although lorises tend to prefer substrates around which their hands can cling completely, the smaller slender lorises will not shy from scaling a tree trunk. Indeed, trunks are amongst the most widely used substrates for *Nycticebus*; slow lorises can cling to trunks of more than 100 cm in diameter for extended periods of up to 45 min, during which time they intensively gouge for gum and other exudates.²² As Dykyj²³ predicted, whether the habitat is sparse or impenetrable, lorises of all species tend to choose branches having similar diameters. Lorises are very busy, constantly moving up and down and back forth. Their average height is habitat-dependent, but all lorises use all heights available, including the highest canopy and the ground if there is no other choice. However, they most commonly are observed below 10 m. The only exception may be the slow lorises from Borneo; it seems that sharing the forest with tarsiers keeps slow lorises at higher forest levels due to interspecific competition.³⁵ No loris moves as little as 15–20 m per night; *Loris* typically moves approximately 1 km per night, whereas *Nycticebus* typically moves more than 5 km more than

most bushbabies do, equalling the ranges of much larger primates such as gibbons.³⁶ Lorises certainly do not live in one tree; rather, they range widely, with a complex system of range overlap.

Lorises are not limited to tropical rainforests. They are found in drought-ridden *Acacia* scrub, montane forests, peat swamps, and even in home gardens with few trees.^{37,38} Their habitats range in monthly mean temperature from 7°–50° C and in altitude from 0–2,000 m asl.¹ In short, lorises use their incredible grasping hands to exploit an incredibly wide variety of ecological niches and, despite a high degree of specialization, also show an extreme degree of flexibility.

GREGARIOUS SOCIETIES

The nocturnal strepsirrhines in general have long been regarded as solitary. despite multiple attempts over the years to thwart the use of this term.^{39–41} Various authors have pointed to the complex systems of home range overlap, mating systems, sleeping groups, and vocal and olfactory communication systems that contribute to varying levels of gregariousness among the nocturnal strepsirrhines.

Slow and slender lorises do not fare well in captivity; not only is mating success low, but fighting often ensues, contributing further to the belief that these animals must be utterly solitary.⁴² Captive cages for these small-bodied animals are often

miniscule⁴³ and, as noted earlier, it may be the restrictions of close proximity, for animals used to ranging over huge areas, that contributes to vicious head wounds and death among captive lorises.⁴²

In fact, all lorises are both social and often gregarious, sleeping in pairs or in groups of up to 8 animals (Box 3), and showing complex patterns of home range overlap. Gray slender lorises have proven to be among the most gregarious of the nocturnal primates, spending up to 38% of their time with another loris.⁴⁹ Similarly, slow lorises spend considerable periods together. Greater slow lorises spent up to 10% of their activity budget in behaviors such as playing, grooming, and feeding together,⁴⁶ whereas Javan slow lorises spent as much as 65% of their time in spatial proximity, including body contact, with an average of 18%.⁴⁷

What has selected for this very social life among lorises is not clear, but what captive studies have clearly shown is that slow and slender lorises are among the most K-selected primates for their body size.⁵⁰ Primates are characterized by very small litters, and their offspring develop slowly in comparison to similarly sized nonprimates.¹³ However, for their size, lorises are extreme in this respect. *Loris* has a gestation of about 165–170 days,^{51,52} and *Nycticebus* 192–203 days.^{50,53} The first estrus of *Loris* does not occur until females are 340 days old, with first birth occurring at 530 days.⁵¹ The interbirth interval

Box 3. Ranging in Lorises.

Previous studies of nocturnal primates used sleep-site location and composition to determine aspects of social organization and home range size.⁷ However, the number of sleeping sites used by male and female lorises is not related to home range size. In the adjoining figure, data are given on the mean 95% MCP home range size and number of sleeping size (+/- 1 s.e.m.) of adult males and adult females, with sample size (number of individuals) in brackets. Dispersing individuals are excluded. Data included are from *Nycticebus pygmaeus*,⁴⁴ *L. l. malabaricus*,⁴⁵ *N. coucang*,⁴⁶ *N. javanicus*,⁴⁷ *L. tardigradus*,⁴⁸ and *L. lydekkerianus*.⁴⁹

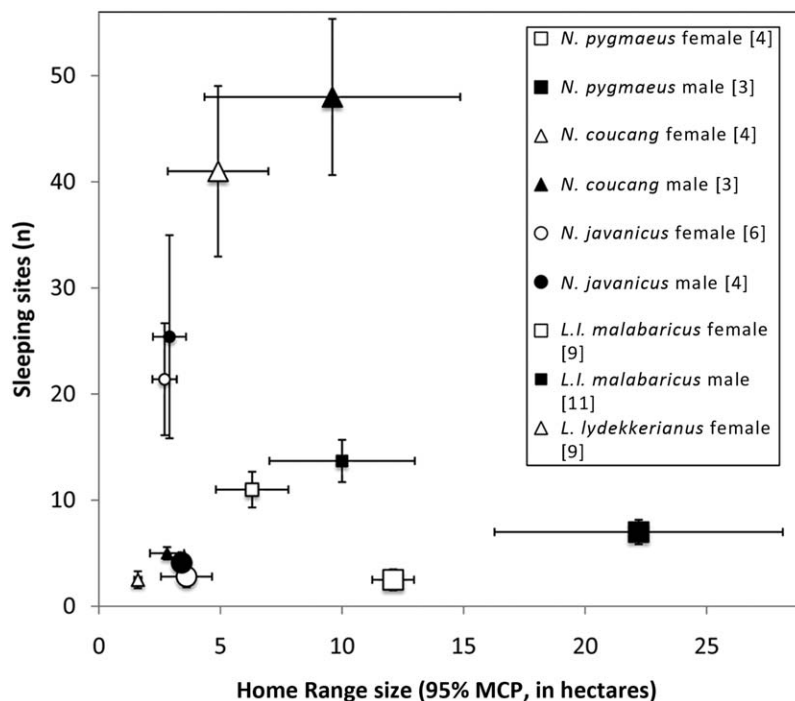
The only clear relationship between the number of sleeping sites slow or slender lorises have is that for all three species of slender and all three species of slow loris males have a larger number of sleeping sites. This coincides mostly, but not exclusively, with larger home range sizes.

L. l. lydekkerianus have small home ranges of 1.5–2.0 (females) and 1.5–3.6 (males) ha, with a handful of sleeping sites that are reguly reused. Males and females show a very similar pattern. *L. tardigradus* have similarly small home ranges (1.2–5.4 ha for females and 1.4–4.1 for males), but use many

more sleeping sites, sometimes more than 40 for a single individual. *L. l. malabaricus* have markedly larger home ranges than do the other slender lorises (4.0–15.3 ha for females and 2.8–34.3 for males), but the number of their sleeping sites is intermediate between *L. lydekkerianus* and *L. tardigradus*.

The variation in home range sizes and sleeping sites is even more pronounced for the slow lorises. *N. javanicus*, in terms of home range size and number of sleeping sites, is more similar to *L. l. lydekkerianus* than to the other slow lorises, and displays little sexual difference. *N. coucang* have intermediate home ranges, but both for males and females a relatively large number of sleeping sites; males have both larger home ranges and use more sleeping sites. *N. pygmaeus* have large home ranges with a limited number of sleeping sites. They show the greatest amount of sexual segregation, with females having significantly smaller home ranges and far fewer sleeping sites.

Some aspects of sleeping site use are similar. The normal sleeping site arrangement across species is an adult female, adult male, and dependent offspring (1–3). Grey slender and pygmy lorises occasionally admit an extra adult male into sleeping sites. No lorises use any form of cavity for sleeping. They all rely instead on the concealment of branch tangles or bamboo clumps, where they cling tightly to the substrate in a species-typical sleep ball of one or more animals.



in *Loris* is around 15 months and in *Nycticebus* 17–22 months, depending on the species.⁵⁰ Sexual maturity in *Nycticebus* does not occur until 540–720 days of age.⁵⁴ In the wild, Javan slow lorises do not disperse until they are 16–18 months old and, even then, may still return

to their parental group, caring for offspring and sleeping with their parents.⁵⁵

From an ecological perspective, diet may also play a role in the tendency toward gregariousness among lorises. For the more faunivorous *Loris*, sharing of gregarious insect

colonies such as ants and termites that are defendable and replenishable may allow for some degree of sociality. For the larger *Nycticebus*, social feeding occurs at two defendable resource sites: gum trees, where gum may be available year-round and at more seasonal floral

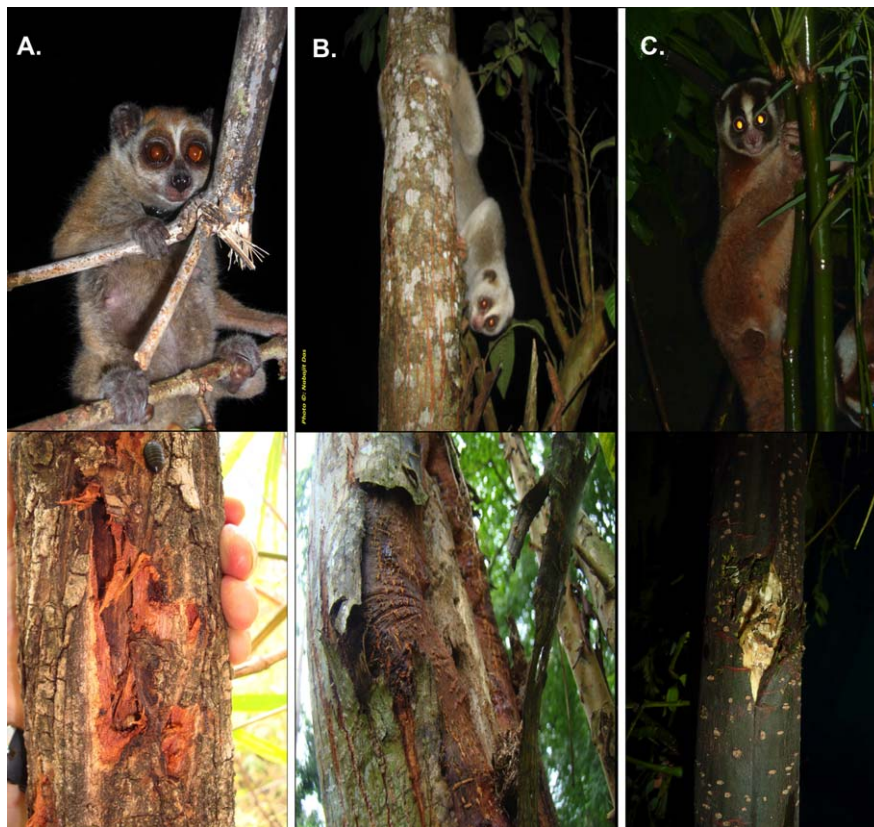
Box 4. Camouflage Coloration in Slow Lorises?

Species	N	% girth covered by dark dorsal hairs
<i>N. pygmaeus</i>	22	38% + 0.04
<i>N. bengalensis</i>	12	42% + 0.10
<i>N. javanicus</i>	21	33% + 0.07
<i>N. coucang</i>	45	34% + 0.10
Bornean lorises	23	34% + 0.10

On the basis of seeing holes in the bark of trees, Tan and Drake⁶⁵ were the first researchers to suggest that slow lorises might include gum in their diet. All wild field studies now confirm that gum is a staple of the slow loris diet. Closer scrutiny

of the morphology of slow lorises makes it surprising that no one ever guessed at this extreme adaptation earlier, since several traits point toward exudativory: a modified stout toothcomb; an enlarged cecum; a long, narrow tongue; hands and feet with large surface area; and u-shaped hind legs.⁶² The dorsal fur of the slow loris may be another factor that is directly linked to exudativory. Streicher⁶⁶ noted that wild-caught *N. pygmaeus* actually changed fur color depending on the seasons, losing their dorsal stripe during times of food abundance and regaining it during times when trees lost their leaves.

Nekaris and coworkers⁶² suggested that this might be a form of camouflage, with the dorsal stripe becoming present when the animal needs to appear less visible. Nekaris and colleagues⁶⁷ examined museum specimens of the dorsal fur of slow loris species, giving particular attention to the percentage of the girth covered by dark camouflaging hair. Comparing the percent of girth covered by dark dorsal hairs, they found that species significantly differed (Table inset). This is probably a result of background matching with their preferred gum tree species, as is shown as the inset photographs (below).



Three slow lorises (above) and their common exudates feeding trees (below): A) *Nycticebus pygmaeus* and unknown genus; B) *N. bengalensis* and terminalia trunk; C) *N. javanicus* and albiza trunk. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

inflorescences where they regularly lap nectar. These unique dietary adaptations may help us to understand aspects of primate evolution.

VISUAL PREDATORS AND PRIMATE POLLINATORS

Primate eyes are placed forward on the face so that the visual fields

overlap, resulting in stereoscopic or binocular vision. Strepsirrhines have less orbital convergence than do haplorhines, but among strepsirrhines

the most convergent and closely approximated orbits are found in the Asian lorises.¹¹ Two main contending hypotheses still vie to explain what ecological drivers may have selected for this trait. Cartmill^{10,56,57} has attested that visual predation – the visual detection, striking at, and capture of prey at close range in the fine branch niche – was the key primate innovation. For the nonleaping lorises in particular, which do not require distance cues to approximate leaps, convergence could evolve to an extreme. Sussman,^{58,59} however, pointed to the complex relationship between trees that are dependent on primates for pollination and the emergence of euprimates almost immediately following the appearance of angiosperms. He concluded that stereoscopic vision was just one of several primate traits needed to exploit the windfall of resources suddenly available in the form of fruits, nectar, and seeds, to be accessed because of vision, olfaction, and manual agility. Primates, being the only nonvolant animals capable of accessing these resources from the swaying terminal branches, would require a suite of traits that would allow them to forage safely in this perilous three-dimensional niche. Incredibly, lorises could be the perfect extreme model for both of these hypotheses.

The first detailed dietary studies of lorises were of *Loris*, and revealed that both species were almost completely faunivorous.^{60,61} Despite occasional sampling of fruits or gum, more than 90% of the diet of *Loris lydekkerianus* in Ayyalur Interface Forestry Division, South India, and 100% of the diet of *L. tardigradus* in Masmullah Proposed Forest Reserve, southwest Sri Lanka, consisted of insects and small vertebrates. As Cartmill^{10,56} had predicted, slender lorises stealthily hunted for their prey, and could be seen to visually hone in on their victims before pouncing with deadly precision. Although hunting occurred in middle sturdy branches too, the terminal branches required different techniques, including catching more acrobatic prey in more energetic postures.⁶¹ Cartmill's

hypothesis regarding forward-facing eyes as an adaptation for catching insects seems vindicated in the case of South Asian lorises.

Then came the first detailed study using radio tracking of slow lorises. Over 28 months, Wiens⁴⁶ recorded 139 instances of feeding by 15 individuals. Unlike *Loris*, the greater slow lorises *N. coucang* he studied consumed mostly exudates (60%), followed by nectar (28%), fruit, and finally arthropods. This was in contrast to his 118 fecal pellets that comprised mainly arthropods, but with traces of wood, indicating exudativory. As nectar consumption and exudate eating are highlighted in his study as obvious behaviors, could his observations have been biased? Could an entire genus of primates that are exudate specialists be overlooked for so long?

Wiens' study was no one-off. Nekaris and coworkers⁶² reviewed twelve subsequent studies highlighting the importance of exudates to *Nycticebus*. Others^{63–65} have added further to this compendium. Slow lorises have proven to be gouging machines, capable of producing large holes in branches and trunks in a matter of seconds, placing them among only a few other primate genera (for example, *Phaner,*

Cebuella, and *Callithrix*) of “true gougers.” Spending up to 45 minutes clinging to a trunk, slow lorises do not need claws or even keeled nails to cling to trunks; instead, their unique hands, strong u-shaped hind legs, and camouflaged fur (Box 4) seem to be adapted for this purpose. Even at the age of about three months, slow lorises gouge (Fig. 3); they may follow their parents to the gum source or, when parked, use scent marks left by their parents at gouge sites that lead to the food source. Individuals may make over 100 holes in a single tree, then return on subsequent nights. Please see video 4 (<https://www.youtube.com/watch?v=SZHG1sijbqM>).

Whereas *Loris* can be seen as a predatory killing machine, *Nycticebus* can be seen as nature's extractor. Most of the 12 studies Nekaris and coworkers reviewed⁶² were of short duration, but all available long-term studies also reveal remarkable adaptations to nectarivory by *Nycticebus*. Having one of the longest tongues (Fig. 4) of any primate coupled with a short, broad sublingual (Fig. 5) bedecked with six to nine denticles,⁶ the loris can insert this pair into many varieties of flowers and lap up the nectar,²² spending an average of 17 seconds per flower and licking as

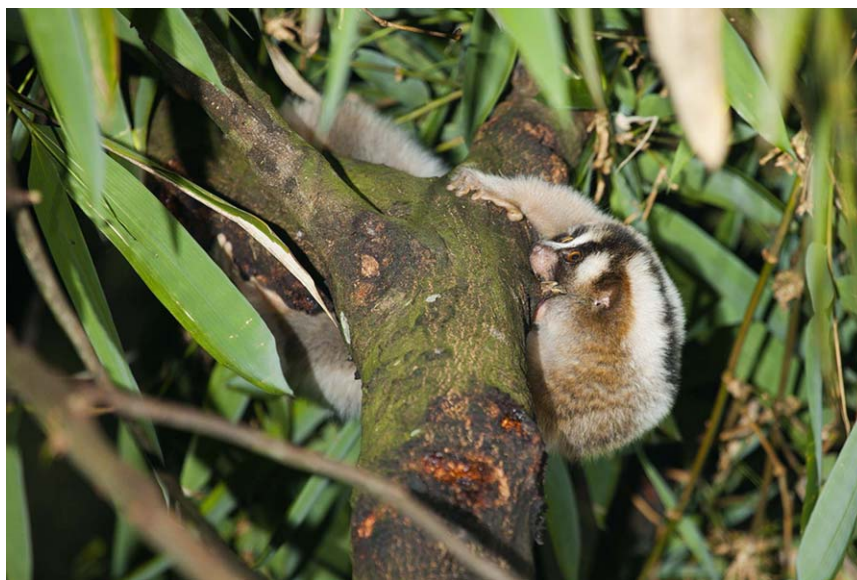


Figure 3. Slow lorises gouge for exudates from about three months of age. The extremely wide gape used to produce large holes in trees (see the hole below the ~300 g loris for size comparison) is demonstrated here by a three-month old Javan slow loris. Photo by M. Williams. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)



Figure 4. A slow loris uses its large tongue to lick exudates. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

many as 100 flowers in a single tree.⁶⁸ The animal emerges with a pollen-covered face and, as it slowly proceeds from one flower to the next, examining each one, it presumably has a role in pollinating these flowers. Please see video 5 (<https://www.youtube.com/watch?v=KLj1RRx5cBY>).

Moore⁶⁸ studied this behavior in the most detail. He found that with delicate precision a slow loris will reel the flower toward its face, lick it intensely, and then slowly reel the branch back



Figure 5. The underside of a slow loris tongue showing the sublingua. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

out without any damage to the flower. In this olfactory milieu, the loris relies almost exclusively on vision to explore the flowers it seeks, visually focusing on each one with a steady gaze. It gently holds each and every flower, carefully maneuvering through the bedlam of possible food items, before selecting particular items.⁶⁸ Cartmill⁵⁷ found it difficult to envision how, in Sussman's original version⁵⁸ of the Angiosperm Coevolution Hypothesis, nectar could play such a vital role in selecting for primate traits. For a loris, tackling a confusing floral array in the swaying terminal branches is just as challenging as catching a flying moth, if not more so.

TOLERANT TO TOXINS

Whatever questions Asia's lorises may help to answer regarding the evolution of primates and their traits, these enigmatic primates possess one more extreme trait that requires analysis in its own right. Both slender and slow lorises are remarkably tolerant to toxins, while the even more extreme slow lorises are toxic themselves. Please see video 6 (<https://www.youtube.com/watch?v=rLAQYpqUcbg>).

Rasmussen and Nekaris⁸ were the first to point out that the remarkably slow life histories of lorises could not be accounted for by body size, sociality, or ecological stability. They proposed that adaptation to a diet containing high levels of toxic compounds, particularly insects, might explain it. Given the difficulties of digesting and processing noxious foods, the reduced basal metabolism, along with their long gestation length and weaning period might be explained by a toxic diet, as has been argued for anteaters, sloths, and their relatives. Nekaris and Rasmussen⁶⁰ went on to show that indeed, Mysore slender lorises were remarkably tolerant to a wide variety of noxious prey in their diet, including a large portion of ants and termites, as well as the even more potent tenebrionid beetles. Kumara, Kumar, and Singh⁶⁹ and Nekaris and colleagues⁷⁰ showed that slender lorises seem to anoint themselves with chemicals from ants; such anoint-

ment may allow slender lorises to exploit social insect colonies through a form of olfactory camouflage.

Can slow life history also be explained by the diet of the slow lorises, which rely largely on gum and nectar? Wiens, Zitzmann, and Hussein³⁷ demonstrated that the saps and nectar consumed by greater slow lorises do indeed contain high levels of secondary compounds that are indigestible by most mammals. Indeed, the bark and gums of some species could either blister human skin or, even in small quantities, kill humans. Das, Nekaris, and Bhattacharjee⁶⁴ confirmed this assertion and, looking at a wider variety of exudates consumed by slow lorises, showed that a large majority of loris-preferred exudates are widely used in human traditional medicines and may be used to kill various parasites. A diet replete with toxins and digestive deterrents could explain numerous slow loris adaptations, from specialized hindgut morphology to their very low basal metabolic rate, which are similar to that found in other mammals that ingest high amounts of toxins.

For the slow lorises in particular, not all of the toxic elements of their food seem to be digested and excreted. Unlike the slender lorises, the slow lorises exhibit what may be the most extreme trait of all: they are the world's only known venomous primates.⁷¹ Slow loris venom is produced when an animal raises its arms above its head and combines saliva with an exudate from its brachial gland (BGE) by moving its head side to side and licking the brachial gland (Fig. 6). The bite of animals born in captivity can severely impair and kill other lorises,⁴² but the bite of wild lorises may be even more severe. Indeed, Nekaris and colleagues⁷⁰ suggest that the sequestration of toxins from wild food, whereby toxic compounds from the food are excreted by BGE or saliva, may supplement loris venom. Indeed, preliminary chemical analyses show that venom from recently wild-caught animals contains batrachotoxins, which are lacking in animals that have been in captivity for a year or more. Similarly, as has been observed in numerous amphibian species, toxic



Figure 6. The slow loris is a venomous primate, as demonstrated by the Javan slow loris. a: the venom is produced when an animal combines saliva with oil from the brachial gland, often by raising its arms over its head; at this point, the loris moves its head extremely rapidly from side to side, combining the two fluids (Photo by A. Walmsley); b: The toothcomb is capable of injecting the venom (Photo by A. Walmsley). c: The receiver may be another loris, the flesh of which may become necrotic as a result of the bite; this adult male was severely wounded after a fight but, remarkably, healed within three months with little scarring (Photo by E. J. Rode). (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

compound sequestration also may be the key that allows injured animals to heal. Interestingly, for recently wild-caught animals in captivity, the bite from a conspecific can be a death sentence, whereas similar wounds can heal remarkably quickly in the wild. Further studies are ongoing, but chemical evidence suggests that the saliva and BGE can operate separately. The multiple functions of the venom may be explained by unique chemical properties in the saliva that are separate from those found in the BGE. Combined, however, the two substances form a new protein, meaning that the chemicals produced by slow lorises are indeed complex, mirroring systems in some frogs and snakes.⁷² The venom, the function of which is still being studied, seems to have multiple uses for slow lorises, including defence against conspecifics, anti-parasite defense, and potential defense against predators.⁷⁰ When and why slow loris venom evolved is only beginning to be understood, but it is possible that during the Miocene, when both *Nycticebus* and cobras (*Naja* spp.) migrated into Asia, the already nonsaltatory slow lorises needed extra defenses when moving across long expanses of open ground. Muellierian mimicry of cobras during this time could explain the origin of this most extreme trait.⁷⁰

EXTREME APPEARANCES

A discussion of lorises would not be complete without alluding to their outward appearance, which has led

to their being the subject of human interest for centuries.⁷³ The huge eyes and almost human-like appearance of these tiny-tailed primates has led to their being considered divine creatures in both South and Southeast Asia. At the same time, their eerie call and fiery eyes have led to their persecution in ritual and superstition, with people stoning them on sight or humans using various loris body parts to cast spells on their enemies. Perhaps the strong association of lorises with medicinal plants that has also led to their use in “curing” or treating more than 100 diseases across their entire range.^{73,74} Indeed, in parts of southeast Asia, the medicinal trade is so rampant that slow lorises have become locally extinct in parts of their range.⁷⁵

A more recent phenomenon relates to the opposite extreme, with slow lorises being considered one of the cutest animals on the planet according to countless media stories. For a long time, slow lorises in particular were the most common protected primates seen in many of Asia’s illegal wild-animal markets.⁷⁶ The local pet trade has now gone global, partially driven by social media. Indeed, the slow loris has gone from obscurity to a household name, with countless viewers on social networking sites driving the demand for illegal trade.⁷⁷ On an international scale, the desire to have these primates as pets has become so alarming that in 2007 they became the first primates in over 20 years to be elevated to Appendix 1 of CITES.⁷⁸ All

species of slow loris are now listed as threatened on the IUCN Red List. Unfortunately, one more term can be added to the description of these primates: extremely rare and endangered.

A SYNTHESIS

Remarkably, within a relatively taxonomically depauperate subfamily, the Lorisinae, we see a remarkable range of body sizes, social behaviors, and dietary adaptations. At the same time, we see a group of primates having extremely flexibility in their ability to cope with different habitat types, substrate choices, and niche breadth. Occurring in almost all forest types, at all strata, and at all altitudes, these most extreme primates still have a lot to offer for aspiring students wishing to address almost any aspect of primate ecology and evolution. Hopefully, any such study will be accompanied with similar efforts to stop their rapid decline in the wild.

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